OBSERVATIONS UPON THE ANATOMY AND RELATIONS OF THE "DUMB-BELL-SHAPED" BONE IN *ORNITHORHYNCHUS*, WITH A NEW THEORY OF ITS HOMOLOGY; AND UPON A HITHERTO UNDESCRIBED CHARACTER OF THE NASAL SEPTUM IN THE GENERA *ORNITHORHYNCHUS* AND *ECHIDNA*.

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(Plates VIII.-IX.)

(A preliminary note summarising most of the conclusions arrived at in this paper was presented at the Meeting of the Society March 28th, 1894, and published in the Abstract of Proceedings of that date).

The question of the morphological significance of the dumb-bell-shaped bone in *Ornithorhynchus* first attracted the attention of the writer when investigating, with Dr. C. J. Martin, the anatomy of the muzzle of this animal. In the paper in the Macleay Memorial Volume (1) in which we recorded the results of our work, no new opinion upon the subject of the present paper was expressed, though even then our series of coronal sections had gone far to convince me that the usual premaxillary theory of the nature of the dumb-bell bone was an inadequate one. This latter view was that entertained by Rudolphi and Meckel (2, p. 20) and was adopted by Owen in his article on the Monotremes in Todd's Cyclopædia (3).

But in his later work upon the Anatomy of Vertebrates (4, p. 322) Owen apparently forsook this theory in favour of an

interpretation of the bone as a 'prenasal ossicle.' This view was adopted by Flower in the earlier editions of the 'Osteology of the Mammalia' (5, p. 219), where the bone is referred to as placed in, or in front of, the anterior extremity of the mesethmoid cartilage, and apparently corresponding to the so-called 'prenasal' of the pig. In 1883 Albrecht (7) again advocated the older (intermaxillary) view of the bone mainly upon reasons derived from a study of the normal and pathological development of the premaxilla in other mammals. The contentions of this author were in 1885 supported by Sir William Turner, who devoted a paper in the Journal of Anatomy and Physiology (8) to a critical examination of the prenasal and intermaxillary theories respectively. His reasons for adhering to the latter are in part founded on his own observations upon the region by means of special dissection. In the edition of the 'Osteology of the Mammalia' published during the same year, 1885, Professor Flower (with Dr. Gadow) explicitly gave up the prenasal theory in favour of the intermaxillary as advocated by Albrecht and Turner. But in the descriptive passage referring to it an extremely misleading description is given of the bone as "placed in front of the anterior extremity of the mesethmoid cartilage in the palatal aspect of the jaw." This statement is indeed quite inconsistent with one of Turner's points of contrast between the dumb-bell bone and a true prenasal, viz., that the latter is (and the former is not) "placed in front of the vomer and mesethmoid cartilage." And in point of fact the dumb-bell bone is entirely ventrad of the cartilaginous septum and far behind the preaxial end of the latter.

The latest contribution to the literature of this subject that I am aware of (apart from the paper in the Macleay Memorial Volume above-mentioned, which only incidentally refers to it) is a paper by Prof. Symington, published in 1891 (9). This author also accepts the view which identifies the dumb-bell bone with an element of the mammalian premaxilla. Both Turner and Symington have recorded important details of the structure and relations of this very interesting ossicle, and the results of their

observations we propose first of all briefly to review, as it is chiefly to these authors that we owe our knowledge of the detailed anatomy of the bone. Symington's chief results were obtained by the study of series of coronal sections.

After referring to its shape, Turner *(loc. cit.)* states that the dumb-bell bone "consists of two symmetrical and lateral halves united mesially by a suture, the line of which may be seen on the palatal surface of the bone, though the two halves obviously become fused at a comparatively early period of life." He also states that it is situated "in the hinder part of a fibrous membrane, which is attached behind to the anterior free border of the palate plate of each superior maxilla, on each side to the inner border of the intermaxilla, &c.," and that "the edge of the dumb-bell bone is surrounded by the membrane." He further states that "the upper surface of the dumb-bell bone lies immediately subjacent to the anterior somewhat expanded end of the vomer, which is fused with it along its mesial line." He then proceeds to refer to its relation to the naso-palatine or incisive foramina, which open on each side of and close to the isthmus or intermediate portion of the dumb-bell bone as seen from the palate, and he concludes that in its relation to the incisive foramina, the dumb-bell bone corresponds with "that portion of the intermaxillary in other Mammalia which lies between the incisive foramen and the mesial palatal suture"; and that "the more anterior part of the roof of the mouth does not undergo an ossific change, but remains as fibrous membrane, except in the limited area where the dumb-bell-shaped bone is produced." He then goes on to examine the argument for the theory that the dumb-bell bone is the homologue of the prenasal bone of the pig, as this was expressed by Flower, following Owen's later view, and he sums up in favour of its correspondence to the mesial element of the premaxilla rather than to the prenasal, as follows:—The dumb-bell-shaped bone "is inferior to the vomer and fused with its inferior border; it has no relation to the anterior nares; it enters into the constitution of the hard palate, and it forms the inner boundary of the entrance into the naso-palatine canal. In its position and relations it

corresponds with that part of the intermaxilla which lies between the incisive canal and the mesial palatal suture." It would appear from the descriptions thus summarised that Sir Wm. Turner regards the dumb-bell bone as consisting merely of a palatine plate, since he considers it to be fused along its mesial line dorsally with the anterior end of the vomer. We shall see presently that the mesial bone rising dorsally, vomer-like, from the palatine dumb-bell is an integral part of the bone itself, and is quite distinct from the true vomer, which ends quite posteriorly to this region. It may also be noted that what Turner has regarded as fibrous membrane filling up the extensive hiatus in the hard palate is in reality a thin sheet of hyaline cartilage forming the floor of the nose, as was shown by Dr. C. J. Martin and the writer in the paper already referred to (1). It is in this cartilaginous layer, and not in fibrous membrane, that the dumb-bell bone is imbedded. Owen and Meckel both refer to this cartilage forming the floor of the nose, and Meckel (2, p. 40) gives its dimensions and attachments as seen from below.

The additional observations of Professor Symington may now be reviewed. He notes the close relation of the upper surface of the anterior nodule of the dumb-bell "to the cartilages of the nose which contain Jacobson's organ," and he further mentions the fact, to which Martin and I have also drawn attention, that near the posterior extremity of the dumb-bell it is covered, as seen from below, by a thin layer of cartilage. As our figure shows, however (1, Pl. XXIII. fig. 17), this is due to the hinder end being more deeply embedded in the cartilaginous nasal floor and not merely grafted upon its under surface as appears, superficially, to be the case in front. From his study of coronal sections Symington has recognised that the bone projecting from the mesial dorsal surface of the palatine dumb-bell is, as has been said above, an integral part of that bone, and his description and figure (9, Pl. XLIII. 2) of a coronal section through the bone near the middle of the posterior nodule will suffice to carry conviction upon this point. In such a section the bone appears "as composed of two crescents with their convexities directed inwards, and the greater

breadth of the bone [in the posterior segment] is due to the elongation of the horns of the crescents which reach about half-way round the organ of Jacobson and are in close contact with its cartilage." This author does not mention the vomer, but quite plainly he does not adopt the view that the vomer is fused with the dumb-bell dorsally.

He concludes by stating that "the dumb-bell bone from its position in relation to the cartilages of the nose is evidently ossified in the membrane investing them," and that "the relation of the bone to the organ of Jacobson corresponds essentially to that of the palatine process of the premaxilla in various mammals" (p. 582).

I may now proceed to state my own observations and conclusions respecting the anatomy of the dumb-bell bone and of the parts related to it.

In studying series of coronal sections one cannot fail to be impressed with the intimate relations between the dumb-bell bone, on the one hand, and Jacobson's organ and the cartilaginous septum nasi, on the other. I have already referred to Symington's account of the relation to the organ of Jacobson, but he has passed over without special remark the relation of the dorsal moiety of the bone to the nasal septum, a relation so marked as to lead Sir Wm. Turner to take that dorsal portion of the bone as part of the vomer.

It may, perhaps, be better to give at once a complete account of the structure and relations of the bone as I have myself determined these both by fresh dissection and by the examination of frontal sections.

In a specially large adult male *Ornithorhynchus* measuring over 50 cm. between the tips of the snout and tail, I find the palatine plate of the "dumb-bell" bone to measure 9·5 mm. in total length. This measurement includes about 2 mm. of the posterior extremity of that plate which is overlapped by the palatine cartilage of the nasal floor (see fig. 1, *b* and *d*) just in front of the anteriorly directed median process of the osseous maxillary palate. The

greater portion of the palatine plate of the dumb-bell lying anterior to this appears as if applied to the ventral surface of the cartilage of the nasal floor, and peripherally it is so applied (*cf.* figs. 1-3 for points referred to in this description). This palatine plate consists of an anterior (*a*) and a posterior (*b*) moiety united by a narrow isthmus (*c*). The isthmus is rather nearer to the anterior than to the posterior end of the plate. The naso-palatine foramen lies on each side opposite and close to the isthmus.

The antero-posterior diameter of the anterior segment, measured to a point opposite the anterior margin of the naso-palatine foramen, is 3·5 mm. Its greatest breadth is 4 mm. The antero-posterior diameter of the posterior segment is 4·5 mm. and its greatest width is 7 mm. Its hinder border forms a nearly semi-circular line. The width of the isthmus is 1·5 mm. The palatine plate is comparatively thin, and the term "dumb-bell-shaped" is only applicable to the general contour of the periphery as seen from below, and indeed it only imperfectly describes that contour.

On dissection to expose the dorsal aspect of the thin palatine plate of the bone, there is seen arising from its dorsal median line a vertical plate (*f*) which dorsally sends out diverging alar laminæ (*g*) on either side. These form the dorsal horns of the "crescents" which Symington has described in transverse sections. The spread of the dorsal alar laminæ at its maximum is 3 mm., and they do not form a horizontal plate, but from their upward divergence they form dorsally a deep median groove or gutter which receives the ventral edge of the cartilaginous nasal septum. The maximum height of this vertical portion of the bone is 2 mm., the maximum height of the bone as a whole being 3 mm. The vertical plate does not extend to the anterior extremity of the horizontal or palatine portion of the bone, but begins about 1·5 mm. behind the anterior end of the latter in a gradually ascending crest with an oblique margin. Just opposite the hinder end of the preaxial segment of the bone the height of the crest is about 1·5 mm. Here it rather suddenly develops its dorsal alar laminæ, and from this point backwards it slightly increases in height, though on the whole its height is fairly uniform and not

exceeding 2 mm. The height does not diminish until the hinder end of the palatine plate of the bone is reached. Here, however, the vertical portion of the bone is continued backwards dorsally for a considerable distance behind the plane of the posterior end of the horizontal palatine plate, in the form of a thick bony spur (*e*), still grooved dorsally for the septum, and gradually undergoing reduction in height at the expense of its ventral border, which becomes elevated more and more dorsally above the horizontal plane of the palate. This spur finally terminates in a posterior bifurcated extremity. The forks (morphologically continuous with the dorsal alar laminæ of the vertical portion of the bone in front) are in contact with the lips of the ventral border of the cartilaginous nasal septum, and they are in continuity posteriorly with the fibres of strong bilateral "vomerine" ligamentous bands of similar sectional area to themselves which connect them with the corresponding forks of the bifid anterior extremity of the vomer. In the dissected specimen from which this description is chiefly taken, the distance between the extreme tips of the forks of the vomer and those of the spur of the dumb-bell bone is about 2 mm., and the latter projects backwards beyond the plane of the posterior extremity of the palatine plate of the dumb-bell for a distance of 4 mm. Now the posterior extremity of the latter bony plate is only about 0·5 mm. in front of the anterior end of the maxillary palate, to which it is usually regarded as articulated ; and accordingly the postaxially directed spur of the dumb-bell bone lies in a horizontal plane above (dorsad of) the maxillary palate, from which indeed it is separated near its hinder end by a vertical distance of about 1·5–2 mm., as is also the bifid anterior end of the vomer and the "vomerine ligament" aforesaid. This interval, spanned by the series of structures just mentioned, is not filled up by any septal structure whatever, but in the living or recent specimen forms a low antero-posteriorly elongated aperture of communication between the two nasal fossæ which is lined by columnar epithelium similar to that lining the adjacent parts of the nasal fossæ (*cf.* fig. 4 *i*). The maximum height of this *internasal* aperture is about 1 mm., while its length antero-

posteriorly is about 5·5 mm.* The plane of the anterior boundary of the internasal passage corresponds pretty accurately with the tip of the median anterior process of the maxillary palate whose upper surface, covered by the nasal mucous membrane, forms the lower boundary of the passage.

When the nasal septum is viewed from the side, the internasal aperture is seen to be overhung and almost concealed by the prominent shelf-like ridge running backwards upon the septum, and forming the posterior continuation of the prominence containing the organ of Jacobson (see figs 4 and 6-8 *gl.*). The roof of the internasal passage may be regarded as considerably widened by the projection of this shelving ridge on either side of the septum (fig. 7 *gl.*).

From what has already been said of the structure of the dumb-bell-shaped bone, it will have become evident that that bone presents on each side a wide and antero-posteriorly elongated sulcus between the lateral portions of its palate plate on the one hand, and the vertical portion of the bone, with its dorsal alæ, on the other (see fig. 3). In this sulcus is lodged the greater part of the organ of Jacobson, enclosed in its incomplete cartilaginous capsule, for which the bone forms a somewhat semi-tubular osseous investment, the tube being incomplete externally (*cf.* figs. 9-11). In transverse sections this gives rise to the appearance of the bone being "composed of two crescents with their convexities directed inwards" (Symington). The hollows of these crescents are, throughout their greater part but not entirely, lined by the investing cartilaginous capsules of the organs of Jacobson. The osseous sulcus on each side is of course deepest where both the width of the palatine plate and the spread of the dorsal alæ are greatest, *i.e.*, in the region of the posterior palatine segment of the bone. It shallows rapidly in front of the naso-palatine foramen through sudden reduction of the alæ, and the more gradual reduction of the vertical plate itself (fig. 12). Posteriorly it is continued

* These measurements are given from the very large specimen chosen for description. In another specimen the length was only about 4·5 mm. It will be understood that all the measurements given are proportionally large.

backwards beyond the posterior segment of the palate plate of the bone as a groove upon the side of the posterior spur, where that lies in the roof of the internasal passage (figs. 7 and 8).

As Symington has shown (*loc. cit. cf.* his pl. XLIII. fig. 1) the organ of Jacobson in *Ornithorhynchus*, with its cartilaginous capsule, is continued forwards for some little distance in front of the naso-palatine foramen into which its duct opens, and in fact it reaches to near the anterior end of the preaxial segment of the dumb-bell ending immediately in front of the anterior commencement of the vertical crest. Posteriorly the organ ends at the plane of the anterior margin of the internasal aperture, *i.e*, that of the anterior limit of the maxillary palate, and only a very short distance behind the plane of the hinder end of the dumb-bell-shaped plate.

The outer wall of its cartilaginous capsule, however, is continued a little further back, closing in externally the continuation, on the posterior spur, of the lateral groove of the bone, in which are lodged the great nerves and the vessels destined for Jacobson's organ. These are contained in the base of the shelving ridge referred to above, but the marginal part of the shelf consists merely of mucous membrane, including an elongated mass of glandular tissue. In sections through the middle of the internasal aperture (fig. 7) the glandular tissue is responsible for about two-thirds of the entire width of the shelf, but at the anterior margin of the passage it forms only about a half of the total width. This definite glandular prominence lies outside the capsule of Jacobson's organ, and may be traced forwards as an extra-capsular prominence on its dorso-lateral wall almost to the anterior end of the organ. A small amount of glandular tissue is, however, to be found within the capsule of the organ.

In the light of these observations I propose now to reconsider the grounds upon which the dumb-bell bone has been so confidently regarded as simply the inner or mesial palatine portion of the intermaxillæ. The criteria which, in Sir Wm. Turner's opinion, were sufficient to establish this judgment, have already been quoted, and we have seen that the first of these depends on an

erroneous view of the relation of the dumb-bell bone to the vomer. This is an extremely important point, and I am surprised that Prof. Symington does not explicitly recognise the mistake which his observations were quite sufficient to correct. It is very plain, both from Symington's observations and my own, that the dumb-bell-shaped bone is not inferior but anterior to the vomer, and that it is *not* "fused with the inferior border" of the latter.

The criteria that remain,—viz., that it "has no relation to the anterior nares," that "it enters into the constitution of the hard palate," and that "it forms the inner boundary of the entrance into the naso-palatine canal"—may be sufficient to disprove the homology to the prenasal bone of the pig. A powerful additional argument against the homology to the prenasal bone in the pig is derived from the observations of Dr. Martin and the writer upon the anterior extension of the cartilaginous septum in *Ornithorhynchus* in the form of a flattened 'prenasal plate' lying in front of the dumb-bell bone and continuous behind with the ventral extensions of the alinasal or aliseptal cartilages which form the cartilaginous nasal floor (1, pp. 185-8). But the reasons adduced do not appear to me sufficient to establish the intermaxillary nature of the dumb-bell bone against the contention that that bone is a true "anterior vomer" formed, of course, by the fusion of two bilaterally symmetrical halves, and this is the view which it is one of the objects of this paper to advocate. Whenever it is recognised that the vertical bony lamella dorsad of the palatine dumb-bell is not part of *the* vomer but an integral part of the so-called dumb-bell bone, certain of the relations and connections of that bone at once suggest difficulties in the way of its explanation as premaxillary.

(1) Although the palatine plate of the dumb-bell bone appears at first sight as if it were situated in the same morphological plane with the maxillary palate behind it, this is not really the case, because the hinder end of the palatine dumb-bell is embedded in and covered ventrally by the cartilage of the nasal floor, in front of the maxillary palate. (See figs. 1 & 9; and also Macleay Memorial Vol. [1], Pl. XXIII. fig. 17.)

(2) That this peculiar relation of the postaxial end of the dumb-bell to the cartilage of the nasal floor is no trivial or insignificant fact, is confirmed by the prolongation backwards of the vertical part of the bone some considerable distance dorsad of the maxillary palate and in relation to the cartilaginous septum. It appears to me that a bone which is so prolonged backwards on a higher plane than the maxillary palate cannot be regarded as developed in the same morphological plane with it, even though anteriorly it has come down so as to occupy the same actual plane.

(3) But further, we have seen not only that the dumb-bell bone is prolonged backwards in the form of a bifurcated (vomerine) splint in relation to the ventral edge of the cartilaginous septum nasi, altogether above the plane of the maxillary palate, but also that this vomerine spur is separated from the maxillary palate by a very peculiar hiatus. In what light are we to regard the internasal passage above referred to? A very little consideration will, I believe, suffice to render this somewhat extraordinary feature of an adult mammalian septum nasi quite intelligible. When the palatal plates of the embryonic maxillary processes coalesce to form the floor of the nasal cavity, they very soon unite with the ventral edge of the internasal septum. This coalescence generally proceeds backwards towards the posterior nares, and before the coalescence of the palate with the septum is complete posteriorly there is a single median choanal passage, *i.e.*, the nasal cavities freely communicate. It is plain that here in *Ornithorhynchus* we have a condition of non-coalescence of the palate with a certain extent of the ventral border of the septum nasi.* But it is notable that this non-union does not occur towards the posterior

* Attention may here be called to the instructive similarities in the general relations of parts between transverse sections through the nasal region of Platypus in the region of the internasal aperture, and similar sections through the nasal region of many embryo mammals passing through the embryonic choanal communication between the two cavities. *Cf.* in particular, figures in Parker's monographs on development of Mammalian skull, *e.g.*, *Edentata* and *Insectivora*, pl. III. figs. 9 and 9*a*. Note especially the ventral relations of the cartilaginous septum to the vomer, &c.

nares, but in front of the vomer. The question arises, why should the failure to unite with the septum have taken place precisely in this region? This is an important question, and I think it may easily be answered if we recognise that the anterior end of the osseous maxillary palate indicates the anterior limit of fusion of the palatal plates of the secondary or permanent palate. In other words the secondary palate ceases somewhat abruptly with the anterior margin of the maxillaries, and in front of this the floor of the nasal cavities is constituted, not by a secondary palatal formation at all, but simply by the ventral parts of the cartilaginous walls of the primary nasal capsules which are intimately bound up with the forward extension of the intertrabecular cartilage forming the cartilaginous septum nasi. This, indeed, is demonstrably the case. The wide area between the diverging premaxillo-maxillary crura in the macerated skull is largely filled up in the recent state by a sheet of cartilage whose composition has been described and figured in the paper already referred to (1), and which has nothing to do with the secondary palate. In ordinary adult mammals the area, which is homologous with this interval, is closed in below the nasal cavities by the premaxillaries, which send inwards and backwards palatine plates* which join the maxillary palate, completing the secondary palate in front. And according to the prevalent theory the dumb-bell bone in *Ornithorhynchus* represents these premaxillary palatine plates, at least in part. I am of opinion, however, that the facts I have adduced respecting the dorsal and posterior relations of the dumb-bell bone tend to negative the view that that bone is an ossification in the morphological plane of the secondary palate, and point distinctly to its homology to a bone of the vomerine series. To sum up this portion of the argument: I regard the secondary palate as ceasing altogether at the anterior margin of the osseous maxillary palatine plate. The failure to develop in front, on the part of the premaxillary moiety of the usual secondary palate, results in the exposure from below of the ventral walls of the cartilaginous nasal capsules, and of the intervening cartila-

* See, however, discussion towards the end of this paper.

ginous nasal septum. The latter, however, is clad for a certain distance forward on its ventral border by a bilaterally symmetrical anterior vomerine splint, distinct from, but in series with, the principal vomer; while in front of this the ventral aspect of the septum is bare—covered only by the mucous membrane of the mouth—and here it descends, flattens dorso-ventrally, and spreads out into a "prenasal plate" of cartilage, which is continuous laterally and behind with the aliseptal cartilages, and in front with the marginal cartilage of the upper "lip." [See paper (1) and figures in Macleay Memorial Volume.]

Further, with regard to the internasal aperture, I regard it as situated in a position quite definitely determined by the course of development, viz., above the extreme anterior end of the secondary palate. It seems less difficult to understand non-coalescence of the septum with the secondary palate either posteriorly or anteriorly than it would be to imagine an arbitrary interruption of the coalescence midway. Posteriorly a persistent median choanal passage would be the result of premature cessation of the process of coalescence, while non-union anteriorly such as we have in the case before us may possibly be explained by supposing that the porterior boundary of the internasal aperture really represents the original starting point of palatal coalescence, and that the extension of the secondary palate in front of that point, at a lower level than the septum, is the product of a later development. Of course the point can only be decided by actual embryological investigation, for which, unfortunately, the material has hitherto not been available.

The anterior boundary of the fenestra is in my view due to a rapid ventral descent of the septum into the roof of the mouth in front of the anterior border of the permanent palate, and I conjecture that it is probably formed somewhat late in development, as the septum undergoes the great anterior elongation which it acquires in the snout of this long-nosed animal.

It might detract from the value of the arguments based upon the posterior relations of the dumb-bell bone to the internasal aperture if it could be contended that the latter may be merely

an adaptive character in this peculiar animal, and one which may not bear all the significance which I attach to it. But this position can hardly be taken up when I am able to state that the feature appears to be a general character of the *Monotremata* since it is also present in the genus *Echidna* (see fig. 5). I have not yet had time fully to investigate the structural relations of the fenestra in the latter type, though the material is in process of preparation. I fully expect that a study of the same region in *Echidna* along parallel lines will throw a fuller light on the whole anatomy of the region, and will, perhaps, enable us to determine what in that animal is the structural homologue to the dumb-bell bone in *Ornithorhynchus*.

After diligent search I have been unable anywhere to find a reference to this very obvious perforation of the wall between the nasal chambers in *Ornithorhynchus* and *Echidna*, or to the persistence of such an aperture in any other mammalian form. I do not think that its presence can ever have been recorded, else its significance would hardly have been overlooked by comparative anatomists.

The aperture does, however, bear a most interesting resemblance to that which in the duck and certain other water birds (15) perforates the septum opposite the external nostrils. This also is a low and anteriorly elongated aperture in the septum at the nasal floor, and the chief *superficial* difference from the internasal aperture in the Monotremes lies in the more anterior position of the aperture in the duck's nose.

It may yet be contended that the considerations which I have hitherto brought forward are, after all, insufficient to enable us finally to dispose of the argument in favour of the homology,—derived from a comparison between their relations to the organ of Jacobson and the naso-palatine foramen,—between the dumb-bell bone in *Ornithorhynchus* on the one hand, and the palatine plate of the ordinary mammalian premaxilla on the other, or rather that portion of the latter which, in the words of Sir William Turner, " lies between the incisive foramen and the mesial palatal suture."

I fully admit the force of such an objection and recognise that if the view advocated in this paper is to be regarded as valid and satisfactory it must be supported by an explanation of the common relationship just referred to and one in which the admitted facts of that relationship are not left out of account.

In attempting to afford such an explanation, reference may in the first place be made to the condition which is common in reptilian forms. The late Prof. W. K. Parker has shown in his Monograph on the structure and development of the skull in *Tropidonotus natrix* (10) that the vomer occupies a position and relation alike to the cartilaginous nasal septum, to Jacobson's organ, and to the opening of the duct of the latter which corresponds to the site of the naso-palatine foramen, exactly similar to the position and relation which we find the dumb-bell bone to occupy in relation to these structures in *Ornithorhynchus*. And identical relations of the vomer may be recognised in others of those reptilian forms in which the organ of Jacobson reaches so high a degree of development. It is then the vomerine element and not the premaxilla which in lower vertebrates possesses those relations which among the majority of adult mammals seem to be possessed by an inner or mesial osseous element of the premaxilla.

Professor Howes has drawn attention to the significance in *Caiman niger* of the very exceptional arrangement due to the intercalation of the bullous anterior free extremities of the vomers in the premaxillo-maxillary region of the palate. He has shown reason for the belief that this bullous palatine lobe of the vomer is to be regarded as the representative of the osseous investment of Jacobson's organ generally present in other reptiles and in mammals. In other crocodilian forms, in which the palatine lobe of the vomer is absent, he found the anterior truncated extremity of the vomer buried in a powerful 'vomerine' ligament which runs forward to the premaxillary region, where its fibres are attached to the periosteum of the premaxillary region and to the palatine process of the premaxilla when such is present. In a young *Alligator mississippiensis* he found the fibres of this liga-

ment partly in continuity with the walls of two fibro-cartilaginous sacs lying within the embrace of the prepalatine foramina, and he considers it justifiable to assume that these sacs, together with the vomerine ligament, form the vestigial remains of the palatine lobes of the vomers in *Caiman niger* with their associated structures. I have referred to these observations in detail because the descent of the anterior lobes of the vomers into the prepalatine region in *Caiman niger* presents a very fair analogy to the descent of the dumb-bell ossification into the prepalatine region in *Ornithorhynchus*. In the latter case, however, the 'palatine lobe' is not absolutely continuous with the main body of the vomer, the continuity being interrupted by the intervention of the bilateral vomerine ligament which has been described above.*

Turning next to the arrangements in the class Mammalia, we may enquire whether developmental conditions amongst other mammalian orders bear out the objection, founded upon the adult condition of the mammalian skull, to our considering the dumb-bell bone as vomerine rather than premaxillary. And this question may, I think, be answered in the negative. A study of Parker's elaborate monographs, especially those dealing with the development of the skull in *Edentata* and *Insectivora* (12), has tended strongly to confirm the idea I had previously formed of the vomerine nature of the bone in question.

Attention may be specially directed to the following amongst Parker's figures—*Tatusia hybrida*, Pl. II. fig. 6 v.', along with the transverse sections in Pl. III. figs. 7 and 8 v'. A later stage of the same, showing the palatine anterior vomers, is figured on his Pl. v. fig. 5 lettered, by mistake, o'.

In the ripe embryonic condition represented on his Pl. VI., fig. 1 shows the palatine anterior vomers considerably restricted in extent and forming that part of the palate which intervenes between the naso-palatine foramen and the "mesial palatal suture." At this stage, however, they appear to be fused with the palatine plate of the premaxillæ.

* This bilateral vomerine ligament is actually figured by Meckel (2, Pl. VII. fig. 11), though his description of the bone and its relations is meagre.

Again, in *Erinaceus europaeus*, the anterior vomers are shown in Pl. XIX. figs. 1, 3, 7 and 8 (v'.), where their intimate relation to the "recurrent cartilages" or cartilaginous capsules of Jacobson's organs is most striking. *Cf.* also the transverse sections, figs. 4 and 5 of Pl. XVIII.

In reference to the anatomy of the region under notice in *Tatusia hybrida*, Parker has made the following observation (*loc. cit.* p. 18):—"The cartilages protecting 'Jacobson's organs' are no longer tubular, but form half a tube, open externally, the organ lying in the outer hollow. But the cartilages themselves have an osseous counterpart protecting them on the inner side and having their shape and direction; these are the 'anterior paired vomers,' bones well known for their large development in the *Ophidia* and *Lacertilia;* they do not represent a divided 'vomer,' proper, which in nearly all Mammalia is well developed also." This description could almost stand for one of the actual conditions in the adult *Ornithorhynchus*, the paired "anterior vomers" being of course fused mesially.

Thus, if Parker's splendid work could be taken as final, there could be little hesitation in identifying the dumb-bell bone as the homologue of the "anterior vomers" described and figured by him in so many edentate and insectivorous types of Mammalia, as well as in the *Ophidia* and *Lacertilia*.

The figures illustrative of Herzfeld's paper on the organ of Jacobson (13) are also worthy of study in this relation, but in the text this author states that he has simply adopted from Balogh (14) the identification of the bone lying mesially to the incisive foramen as palatine process of premaxilla. Some of the figures, however, show a dorsal extension of this osseous region which is at least highly suggestive of a true vomerine character.

Professor Howes, however, has stated *(loc. cit.)* the opinion that Parker's views respecting the various elements of the vomerine series in the Mammalia are not entirely devoid of uncertainty, and in particular he holds that Parker has "shown that he was unable to draw a sharp distinction between the palatine processes of the premaxillæ and his anterior paired or lateral vomers." Never-

theless, this inability can only be regarded as manifested in certain cases, and Howes himself accepts from Parker certain conclusions on this subject which he sums up as follows:—"(*a*) That we can no longer regard those structures ordinarily described among mammals as 'palatine' processes of the premaxillæ as throughout homologous; and (*b*) that the latter are, in a number of cases, no parts of the premaxillæ at all, but rather referable to the vomerine category;" and he adds that "in his discovery of the complex nature of the (non-pathological) premaxilla of mammals Parker is at one with Albrecht, who has shown that there is reason for regarding the premaxillæ of the adult *Ornithorhynchus* as a combination of distinct elements." The author then proceeds as follows:—"All those mammals for which Parker has recorded the presence of 'anterior paired vomers' are long-nosed. Comparison of the skulls of adults with those of the young as figured by him, will show that while the bones in question may in some cases pass over to the true vomers they more generally remain exclusively related to Jacobson's organ, which they ensheath in the form of the so-called premaxillary palatine processes, and their products of fusion and metamorphosis lie, for the most part, within the area of the latter as ordinarily described." I have quoted at this length from Professor Howes' valuable paper because it appears to me that the condition in *Ornithorhynchus* may be easily interpreted in the light of the last few sentences. *Ornithorhynchus* is a long-nosed mammal whose 'anterior vomers' have fused together in development *without* uniting with any other osseous element. Posteriorly they preserve an intimate relation to the ventral edge of the septum nasi, while anteriorly they constitute exclusively the osseous investment for the cartilaginous capsules of the organs of Jacobson.

In view of Howes' statements above quoted, and of his further dictum that "the vomers and palatine processes of the premaxillaries have been sufficiently shown to be serial elements of a common category," it is not strictly accurate to regard the vomerine view of the dumb-bell bone as really a novel one. But I am unaware that anyone has ever explicitly applied this inter-

pretation to the "os paradoxum" in *Ornithorhynchus*, and the definition of it as a true premaxillary element certainly holds the field. At the same time, when the significance of the statements of Parker and Howes for the interpretation of the premaxilla of other mammals is borne in mind, it may be necessary to admit that the distinction of the dumb-bell bone as vomerine rather than premaxillary is largely a nominal one. I submit, nevertheless, that this nominal distinction is an important one, and I am inclined to hold that a full recognition that here in *Ornithorhynchus* the bone lying between the incisive or naso-palatine foramen and the mesial palatal suture is truly vomerine and has in its origin nothing to do with the body of the premaxilla, will help us to clearer views upon the constitution of the corresponding region in mammals generally.

[See Appendix, p. 150.]

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EXPLANATION OF FIGURES.

PLATE VIII.

Fig. 1.—View of dumb-bell-shaped bone of *Ornithorhynchus* from below, showing palatine plate and vomerine spur, enlarged four diameters.

Fig. 2.—View of dumb-bell-shaped bone from the left side (× 4).

Fig. 3.—View of dumb-bell-shaped bone from the left and above (× 4).

Fig. 4.—Sagittal section of anterior part of snout of adult *Ornithorhynchus*, parallel with and to the right of the mesial plane. The section

passes through the right nostril and exposes the right side of the septum nasi. The internasal aperture is seen below the level of the longitudinal ridge running backwards from Jacobson's organ. The capsule of the latter has been shaved by the section at its most bulging part. The arrow points up towards the naso-palatine foramen.

Fig. 5.—Sagittal section of snout of *Echidna* to left of mesial plane, passing through left nostril, showing nasal septum with its longitudinal ridge and internasal aperture.

References to figs. 1-5.

a, anterior segment; *b*, posterior; *c*, isthmus; *d*, line on posterior segment indicating anterior limit of plate of cartilage which clothes the inferior surface posteriorly; *e*, bifurcated vomerine spur; *f*, vertical part of bone; *g*, dorsal ala; *h*, nostril; *i*, internasal aperture; *j*, Jacobson's organ; *k*, marginal cartilage of upper lip.

PLATE IX.

Figs. 6-12.—Coronal sections through snout of *Ornithorhynchus*. These figures have been drawn on a reduced scale of one-half from photomicrographs having a magnification of eleven diameters.

Fig. 6.—T.s. in plane of posterior boundary of internasal aperture. The bone clothing the cartilaginous septum ventrally is the vomer (main vomer), and it is seen just meeting the dorsal crest of the maxillary palate.

Fig. 7.—T.s. through about the middle of the internasal aperture. Ventrad of the septum are the forks of the vomerine spur of the dumb-bell-shaped bone separated by a little fatty tissue.

Fig. 8.—T.s. through plane of anterior boundary of internasal aperture. The vomerine spur of the dumb-bell is becoming more ventrally placed and is connected with the cartilage just in front of apex of the median process of the osseous maxillary palate by means of some fibrous tissue. The posterior extremity of Jacobson's organ is cut through on either side.

Fig. 9.—T.s. in plane of hinder end of posterior segment where that is still covered below by the cartilaginous lamina of the nasal floor.

Fig. 10.—T.s. through snout, cutting postaxial segment of dumb-bell-shaped bone in front of line *d* in fig. 1.

Fig. 11.—T.s. through snout in plane of naso-palatine foramina and isthmus of dumb-bell bone.

Fig. 12.—T.s. snout in plane passing through hinder portion of preaxial segment and commencement of vertical crest of bone. Here the organ of Jacobson is about its widest.

Lettering of figs. 6-12.

mx., maxillary palate; *m. mx.*, median anterior process of maxillary palate; *v.*, vomer; *d. b. v.*, vomerine spur of dumb-bell bone; *d. b. p.*, posterior segment of dumb-bell bone; *d. b. a.*, anterior segment of dumb-bell bone; *d. b. i.*, isthmus of dumb-bell bone; *J. o.*, organ of Jacobson; *gl.*, glandular ridge; *nn.*, nerves; *n. p. f.*, naso-palatine foramen; *n.c.*, nasal cavity; *a. s.*, ali-septal cartilage; *n. f.*, cartilage of nasal floor; *n. s.*, nasal septum; *i. a.*, internasal aperture.

The figures were drawn by Mr. G. H. Barrow, those of the dumb-bell-shaped bone from nature, those of the coronal sections from photo-micrographs.

Appendix *(July 23rd, 1894)*:—Just on the eve of the final revision of the proofs of the foregoing pages there came to hand by the English mail, P.Z.S. 1894, Part 1 (June 1st), containing Prof. W. Newton Parker's paper, "On some Points in the Structure of the Young of *Echidna aculeata*," to which the Editor has kindly called my attention. In this paper the author refers to the internasal aperture described above and states that "a communication between the two nasal cavities has been described by Home in *Ornithorhynchus*. Zuckerkandl was unable to observe this; but I have satisfied myself that both Monotremes agree in this respect, and that the left and right nasal chambers communicate by a slit-like passage beneath the septum just behind Jacobson's organ." In view of these observations I can only regret that it is impossible now to withdraw the words "hitherto undescribed" from the title of my paper. It is curious that Home's observation should have been passed over in silence by well nigh every later writer on *Ornithorhynchus*.

The present paper was communicated to the Linnean Society of N.S.W. at its meeting on 25th April, 1894, a preliminary note having been read at the previous meeting on 28th March. Professor Parker's paper, although published only on 1st June, 1894, was received by the Zoological Society of London on 7th Nov., 1893, and read at the Society's meeting on 16th Jan., 1894.